Multivariate analysis of variations in intrinsic foot musculature among hominoids

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Abstract

Comparative analysis of the foot muscle architecture among extant great apes is important for understanding the evolution of the human foot and, hence, human habitual bipedal walking. However, to our knowledge, there is no previous report of a quantitative comparison of hominoid intrinsic foot muscle dimensions. In the present study, we quantitatively compared muscle dimensions of the hominoid foot by means of multivariate analysis. The foot muscle mass and physiological cross-sectional area (PCSA) of five chimpanzees, one bonobo, two gorillas, and six orangutans were obtained by our own dissections, and those of humans were taken from published accounts. The muscle mass and PCSA were respectively divided by the total mass and total PCSA of the intrinsic muscles of the entire foot for normalization. Variations in muscle architecture among human and extant great apes were quantified based on principal component analysis. Our results demonstrated that the muscle architecture of the orangutan was the most distinctive, having a larger first dorsal interosseous muscle and smaller abductor hallucis brevis muscle. On the other hand, the gorilla was found to be unique in having a larger abductor digiti minimi muscle. Humans were distinguished from extant great apes by a larger quadratus plantae muscle. The chimpanzee and the bonobo appeared to have very similar muscle architecture, with an intermediate position between the human and the orangutan. These differences (or similarities) in architecture of the intrinsic foot muscles among humans and great apes correspond well to the differences in phylogeny, positional behavior, and locomotion.

Key words: human; great apes; physiological cross-sectional area; principal component analysis.

Introduction

Among primates, great apes are our closest living relatives, providing a unique opportunity to investigate the evolution of morphological adaptations of the hominoid foot. Whereas most modern humans typically engage in only one locomotor mode (habitual bipedalism; Harcourt-Smith & Aiello, 2004), great apes spend their time in the trees and utilize a versatile locomotor repertoire such as quadrumanous climbing, brachiation, and quadrupedalism (Cant, 1987; Doran, 1992, 1993; Hunt, 1992; Doran & Hunt, 1994; Remis, 1995; Thorpe & Crompton, 2006). The foot, as the terminal link in the hindlimb, interacts with the locomotion substrates, and therefore reflects the locomotor behavior of the species. Based on comparative anatomical analyses between humans and great apes, anthropologists and morphologists have discussed form–function relationships in the hindlimb and the evolution of human bipedal locomotion (e.g. Morton, 1924; Straus, 1930; Schultz, 1963; Tuttle, 1970; Ishida, 1972; Bojsen-Møller, 1979; Lewis, 1980a,b; Gomberg, 1981, 1985; Rose, 1988; Aiello & Dean, 1990; Thorpe et al. 1999; Marchi, 2005, 2010; Vereecke et al. 2005; Klenerman & Wood, 2006; Payne et al. 2006; Lovejoy et al. 2009;

Kanamoto et al. 2011; Myatt et al. 2011; Ward et al. 2011; Zipfel et al. 2011; Proctor, 2013; Parr et al. 2014).

In comparative and quantitative studies of the foot muscles of humans and great apes, the focus has been mainly on the extrinsic muscles, demonstrating that humans possess the larger plantar flexors and smaller extrinsic toe flexors (Ishida, 1972; Gomberg, 1981; Thorpe et al. 1999; Vereecke et al. 2005; Payne et al. 2006). These differences can be interpreted as adaptations to provide a propulsive power during bipedal walking and the lack of the ability to grasp with the human hindlimb. However, such studies of the intrinsic foot muscles are very scarce (Gomberg, 1981) and therefore detailed information on the differences in these muscles among these groups is limited to qualitative anatomical traits (Hepburn, 1892; Straus, 1930; Tuttle, 1970; Gomberg, 1981; Aiello & Dean, 1990).

In hominoids, chimpanzees are more similar to humans than orangutans with regard to the better development of the abductor hallucis muscle (Aiello & Dean, 1990; Oishi et al. 2012). On the other hand, chimpanzees, like other great apes, are distinct from humans in having a powerful transverse part of the adductor hallucis muscle (Straus, 1930; Aiello & Dean, 1990). Based on the individual intrinsic foot muscles, the similarities or the differences in hominoid feet depend on the choice of muscle. Thus, our interpretations of the foot muscles of hominoids are limited to isolated aspects because we have yet to explore systematically the overall tendencies among hominoids when using all the intrinsic foot muscles together. Multivariate statistical methods allow the extensive assessment of morphology and can help us to understand such tendencies regarding interspecific morphological variation. Consequently, such techniques have been widely applied in physical anthropology to characterize morphological variations of foot bones (e.g. Kanamoto et al. 2011; Zipfel et al. 2011; Proctor, 2013; Parr et al. 2014). These approaches may also be effective for obtaining a better insight into an evolutionary context of the hominoid foot musculature because locomotor capabilities are determined by the structure and function of both the skeletal and muscular systems. To date, however, to our knowledge, such multivariate statistical methods have never been applied for characterization of the muscle architecture of the foot, mainly due to the limited availability of quantitative information about intrinsic foot muscles of great apes.

The aim of the present study was to quantify variations in muscle architecture of the intrinsic foot muscles among humans and extant great apes based on principal component analysis (PCA). Specifically, we measured muscle mass and muscle fascicle length. The physiological cross-sectional area (PCSA) was also calculated to quantify the force-generating capacity of each of the muscles (Close, 1972; Zajac, 1992). For multivariate analyses, we added data obtained from new dissections to our previously published data on intrinsic foot muscles (Oishi et al. 2009b, 2012). Data from human foot muscles were taken from published accounts.

Differences in locomotor behavior generally correspond to differences in the morphology of the locomotor apparatus. Therefore, it is hypothesized that there exist differences in muscle architecture of the intrinsic foot muscles among hominoids that correspond to different locomotor behaviors, since the foot is the most distal organ that directly interacts with the ground or substrate during locomotion, and hominoids utilize a diverse locomotor repertoire such as quadrumanous climbing, knuckle-walking, and bipedal locomotion. Specifically, we hypothesized that the muscle architecture of the human intrinsic foot muscles would be the most distinctive among extant hominoids since humans are the only species that adopts habitual bipedal walking and does not retain the gripping capacity of the foot. On the other hand, differences in muscle architecture could be attributed to phylogenetic distance as well. Therefore, we also hypothesized that the muscle architecture of orangutans would be the most distinctive among hominoids, and that of humans and African apes would be similar to one another.

Materials and methods

For the multivariate analysis of the intrinsic foot musculature, we obtained the muscle mass and PCSA of intrinsic foot muscles from five chimpanzees, one bonobo, two gorillas, and six orangutans. The data of four chimpanzees (C1, C3, C4, and C5), one gorilla (G1), and two orangutans (O4 and O5) were taken from our previous studies (Oishi et al. 2009b, 2012), but the rest of the data were newly obtained by dissecting additional specimens, as presented in Table 1. The bonobo is the property of the Japan Monkey Centre (Aichi, Japan). Other specimens were donated to the Primate Research Institute, Kyoto University, Osaka Museum of Natural History or the National Museum of Nature and Science (Tokyo, Japan) from the Chausuyama Zoo, Yamajiboku, Tama Zoological Park, Ueno Zoological Gardens, Kamine Zoo, Tennoji Zoo, Higashiyama Zoo and Botanical Garden, and Yokohama Zoological Gardens.

The specimens listed in Table 1 were dissected and muscle dimensions were determined as described in our previous reports (Oishi et al. 2009a,b, 2012). During dissection, the muscles shown in Fig. 1 and Table 2 were exposed and removed from the foot bones. The muscle belly mass (i.e. mass) was measured using an electronic balance. Each muscle belly was immersed in 10% formalin and pinned on cardboard at both ends to prevent shrinkage during fixation. Muscle fascicle length was measured at two to six places dissected in varying locations within the muscle belly using calipers, and the mean value was calculated. The physiological cross-sectional area (PCSA) was calculated by dividing muscle volume by fascicle length. Muscle volume was obtained by dividing muscle mass by muscle density (1.0597 g cm^{-3}; Mendez & Keys, 1960). The pennation angle (the angle between the direction of the muscle fibers and the tendon) was not included in the calculation of PCSA because it was difficult to determine correctly a representative two-dimensional angle from the angle of the three-dimensional fascicle within a muscle. Moreover, in hominoids the pennation angle is generally $< 30°$ in foot muscles (Thorpe et al. 1999; Ledoux et al. 2001). The muscle force along the line of action of the tendon depends on the cosine of the pennation angle, which is approximately 1.0 in these

Table 1 General specimen data.

	C6	B1	G2	O6	O7	O8	O9
Species	Pt	Ppa	Ggg	Ppy	Pa	Ppy	Ppy
Sex	F	M	M	F	M	M	F
Age at death (year)	ca. 47	ca. 29	ca. 34	ca. 43	13	21	ca. 11
Body weight at death (kg)	54.6	–	118.5	67.8	91.6	–	–
Cause of death	Unkown	CD	CD	Unkown	CD	P	DD
Preservation	Frozen	Frozen	Frozen	Frozen	Frozen	Frozen	Frozen
Side	Left	Left	Right	Left	Right	Right	Right
Total muscle mass of foot (g)	143.5	161.4	275.7	241.8	410.3	251.4	175.6

Subjents: Pt (*Pan troglodytes*), Ppa (*Pan paniscus*), Ggg (*Gorilla gorilla gorilla*), Pa (*Pongo abelii*), Ppy (*Pongo pygmaeus*). Cause of death: CD, cardiovascular disease; P, pneumonia; DD, digestive disease.
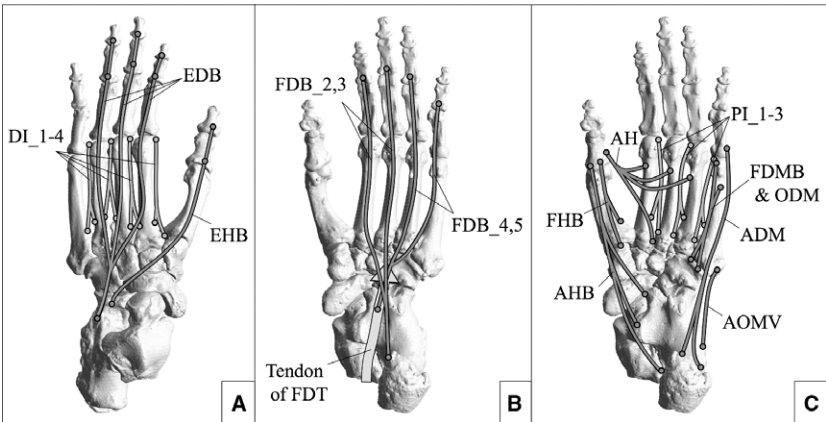
Fig. 1 Schematic diagram of the intrinsic foot muscles of the lowland gorilla in dorsal (A) and plantar (B,C) views. ADM, *M. abductor digiti minimi*; AH, *M. adductor hallucis*; AHB, *M. abductor hallucis brevis*; AOMV, *M. abductor ossis metatarsi V*, DI, *M. dorsal interosseous*; EDB, *M. extensor digitorum brevis*; EHB, *M. extensor hallucis brevis*; FDB, *M. flexor digitorum brevis*; FDMB & ODM, *M. flexor digiti minimi brevis & M. opponens digiti minimi*; FDT, *M. flexor digitorum tibialis* (*M. flexor digitorum longus*); FHB, *M. flexor hallucis brevis*; Lu, *M. lumbricalis*; PI, *M. plantar interosseous*.

muscles. Thus, including the pennation angle would have little effect on our estimations of PCSA (Burkholder et al. 1994). Because we did not have a chance to dissect human feet, human data were obtained from cadaveric studies reported by Silver et al. (1985) and Kura et al. (1997).

To normalize the influence of body size, the mass of each muscle was divided by the total intrinsic muscle mass of the foot to calculate the mass fraction. The PCSA fraction was calculated in the same way. The muscle parameters were not normalized by body mass as in other similar studies, assuming a geometric scaling (Thorpe et al. 1999; Carlson, 2006; Payne et al. 2006) or an allometric scaling (Myatt et al. 2011, 2012). The reason for this was that body mass can vary independently of a skeletal dimension due to such factors as nutritional status, aging, and captivity conditions and may not always be suitable as a baseline.

To determine which muscles contribute the most to variation in the foot muscle architecture, a principal component analysis (PCA) was performed. Specifically, principal components (PCs) of variations in muscle mass (and PCSA) fractions among the specimens were computed based on the variance–covariance matrix. Nonparametric Kruskal–Wallis analysis ($P < 0.05$) was used to test for differences in the PC scores in cross-species comparisons, since the sample size was small and normality of the data could not be assumed. *Post hoc* analyses included Dunn's multiple comparisons with a Bonferroni correction (adjusted $\alpha = 0.05/10 = 0.005$). All statistical analyses were performed using PAST software, version 3.16 (http://folk.uio.no/ohammer/past; Hammer et al. 2001).

Results

Measured muscle mass, PCSA, and fascicle length of all intrinsic foot muscles in newly dissected specimens are presented in Table 2. Comparisons of the mass and PCSA fractions of the intrinsic foot muscles among hominoids are presented in Tables 3 and 4, respectively. For the digiti minimi muscles, the mass fractions were larger in humans and gorillas, and the digital flexor muscles had the highest mass fraction in humans. In the orangutans, the mass fractions of the interosseous and the pedal digital extensor muscles were largest, whereas those of the hallucal muscles were smallest (Table 3). The PCSA fractions exhibited similar tendencies (Table 4).

Table 2 Dimensions of intrinsic foot muscles in great apes.

	Abbreviation	C6 Mass (g)	C6 PCSA (cm²)	C6 FL (cm)	B1 Mass (g)	B1 PCSA (cm²)	B1 FL (cm)	G2 Mass (g)	G2 PCSA (cm²)	G2 FL (cm)
Extensor hallucis brevis	EHB	3.6	1.02	3.3	7.6	1.79	4.0	8.2	2.19	3.5
Extensor digitorum brevis_2	EDB_2	3.3	0.77	4.0	4.8	1.11	4.1	5.4	1.50	3.4
Extensor digitorum brevis_3	EDB_3	4.4	1.14	3.7	3.2	0.82	3.6	6.0	1.46	3.9
Extensor digitorum brevis_4	EDB_4		NP		2.5	0.75	3.1	4.7	1.14	3.9
Flexor digitorum brevis_2	FDB_2	6.8	1.28	5.0	6.6	1.27	4.9	8.0	1.58	4.8
Flexor digitorum brevis_3	FDB_3	6.5	1.22	5.0	9.9	1.90	4.9	17.7	3.87	4.3
Flexor digitorum brevis_4	FDB_4	0.9	0.40	2.1	2.6	1.26	2.0	6.8	2.01	3.2
Flexor digitorum brevis_5	FDB_5	1.3	0.46	2.7	0.2	0.13	1.5	0.6	0.32	1.6
Abductor hallucis brevis	AHB	26.7	5.40	4.7	26.5	5.00	5.0	42.2	7.65	5.2
Flexor hallucis brevis	FHB	12.6	4.93	2.4	10.6	4.51	2.2	23.7	11.09	2.0
Adductor hallucis	AH									
Oblique head	AH_O	10.6	3.28	3.1	13.6	3.63	3.5	20.9	5.57	3.5
Transverse head	AH_T	20.2	4.23	4.5	18.6	3.34	5.3	19.2	2.87	6.3
Abductor digiti minimi	ADM	7.4	2.69	2.6	12.2	5.24	2.2	37.3	18.22	1.9
Flexor digiti minimi brevis & Opponens digiti minimi	FDMB & ODM	2.4	2.35	1.0	4.6	3.19	1.3	9.6	5.63	1.6
Dorsal interosseous_1	DI_1	6.8	2.58	2.5	6.1	3.30	1.7	9.8	4.99	1.9
Dorsal interosseous_2	DI_2	5.6	2.23	2.4	3.9	2.81	1.3	9.4	7.67	1.2
Dorsal interosseous_3	DI_3	5.3	2.01	2.5	4.7	2.71	1.6	9.0	7.24	1.2
Dorsal interosseous_4	DI_4	5.7	2.18	2.5	5.8	3.63	1.5	10.6	8.01	1.2
Plantar interosseous_1	PI_1	3.7	1.76	2.0	4.6	3.40	1.3	6.5	5.51	1.1
Plantar interosseous_2	PI_2	2.9	1.04	2.6	2.7	2.26	1.1	4.7	4.62	1.0
Plantar interosseous_3	PI_3	1.7	0.92	1.7	2.5	2.05	1.2	4.5	4.35	1.0
Lumbricalis_1	Lu_1	1.1	0.24	4.4	2.0	0.35	5.3	1.7	0.57	2.8
Lumbricalis_2	Lu_2	1.8	0.38	4.5	1.9	0.39	4.6	3.2	0.74	4.1
Lumbricalis_3	Lu_3	1.5	0.28	5.1	1.6	0.28	5.3	2.4	0.50	4.4
Lumbricalis_4	Lu_4	0.7	0.13	5.1	1.6	0.32	4.6	2.0	0.37	5.0
Quadratus plantae	QP		NP		0.7	0.17	4.0	2.0	0.48	3.8

Abbreviation	O6 Mass (g)	O6 PCSA (cm²)	O6 FL (cm)	O7 Mass (g)	O7 PCSA (cm²)	O7 FL (cm)	O8 Mass (g)	O8 PCSA (cm²)	O8 FL (cm)	O9 Mass (g)	O9 PCSA (cm²)	O9 FL (cm)
EHB		NP		7.2	1.14	6.0	3.7	0.55	6.4	4.3	0.89	4.6
EDB_2	11.9	2.18	5.2	13.9	1.97	6.7	10.1	1.62	5.9	11.4	2.93	3.7
EDB_3	9.4	1.69	5.2	12.0	1.63	7.0	6.2	0.93	6.3	4.6	1.00	4.3
EDB_4	9.7	1.79	5.1	18.6	2.78	6.3	7.9	1.05	7.1	8.6	1.87	4.3
FDB_2	14.0	2.97	4.4	26.2	3.39	7.3	14.9	2.51	5.6	7.5	1.64	4.3
FDB_3	9.9	2.05	4.6	21.1	2.79	7.1	15.4	2.48	5.8	11.0	2.27	4.6
FDB_4		NP		8.7	1.05	7.8		NP		1.4	1.24	1.1
FDB_5	1.0	0.43	2.2	1.5	0.54	2.6	0.9	0.40	2.2		NP	
AHB	10.9	2.99	3.4	30.1	4.90	5.8	20.7	3.26	6.0	13.5	3.00	4.2
FHB	20.6	8.53	2.3	28.8	9.38	2.9	20.3	6.15	3.1	9.7	5.43	1.7
AH												
AH_O	18.4	3.62	4.8	24.4	3.94	5.8	15.8	2.33	6.4	10.4	2.95	3.3
AH_T	17.3	3.25	5.0	49.9	6.47	7.3	17.9	3.00	5.6	16.7	3.60	4.4
ADM	13.5	8.12	1.6	24.3	6.88	3.3	12.4	3.58	3.3	5.8	2.55	2.1
FDMB & ODM	6.7	5.40	1.2	12.7	7.46	1.6	11.9	4.23	2.7	7.9	4.11	1.8
DI_1	27.8	11.83	2.2	36.4	10.81	3.2	22.3	6.49	3.2	18.8	7.63	2.3
DI_2	16.8	6.83	2.3	19.0	5.91	3.0	12.2	4.75	2.4	7.8	3.66	2.0
DI_3	10.5	5.01	2.0	13.4	4.65	2.7	10.3	3.71	2.6	5.7	2.76	1.9

(continued)

Table 2. (continued)

Abbreviation	O6			O7			O8			O9		
	Mass (g)	PCSA (cm²)	FL (cm)	Mass (g)	PCSA (cm²)	FL (cm)	Mass (g)	PCSA (cm²)	FL (cm)	Mass (g)	PCSA (cm²)	FL (cm)
DI_4	10.1	4.68	2.0	13.7	4.67	2.8	11.0	4.23	2.5	7.4	3.98	1.8
PI_1	10.3	5.03	1.9	11.2	4.40	2.4	10.7	4.16	2.4	4.6	2.43	1.8
PI_2	7.1	3.05	2.2	7.7	2.32	3.1	6.6	1.93	3.2	4.1	1.56	2.5
PI_3	1.7	1.01	1.6	5.3	1.77	2.8	3.3	1.35	2.3	2.7	1.33	1.9
Lu_1	5.5	0.48	10.8	6.0	0.62	9.1	4.5	0.38	11.2	2.6	0.38	6.4
Lu_2	5.0	0.50	9.4	8.6	0.83	9.8	5.7	0.44	12.1	4.1	0.54	7.1
Lu_3	2.9	0.29	9.3	6.1	0.54	10.6	4.2	0.29	13.5	3.4	0.40	8.1
Lu_4	0.8	0.08	9.9	3.5	0.35	9.5	2.6	0.20	12.3	1.6	0.26	5.9
QP	NP			NP			NP			NP		

FL, fascicle length; NP, muscle not present; PCSA, physiological cross-sectional area. The dorsal interosseous muscles of B1 were arranged around the second digit, while those of other great apes were arranged around the third (C6, G2, O6, O8, O9) or fourth digit (O7).

Based on a scree plot and a threshold of 5% of variance explained, the first three components were dominant in the PCA for the mass fractions and in the first four components for the PCSA fractions. These PCs explained cumulatively over 80% of the variation in the sample for the mass and PCSA fractions, respectively.

Results from a PCA of the 24 muscle mass fractions are presented in Fig. 2 as plots of the first principal component (PC1) vs. PC2, and vs. PC3. PC1 accounted for 62.0% of the total variance, PC2 for 20.1%, and PC3 for 5.8%. Figure 2 demonstrates that orangutans were separated from humans and other great apes along PC1, and humans were separated from African great apes along PC2. When a Kruskal–Wallis analysis for PC scores was performed, there were significant differences in PC1 and PC2 for the mass fractions. Although no *post hoc* multiple comparisons for PC1 achieved significance (Bonferroni adjusted $\alpha = 0.005$), the PC2 score was significantly different between humans and chimpanzees. The factor loading shown in Table 5 demonstrated that PC1 was related to the abductor hallucis brevis muscle and the first dorsal interosseous muscle; PC2 was related to the adductor hallucis muscle and the quadratus plantae muscle. Although there was no statistical difference in PC3, gorillas tended to be separated from other hominoids as shown in Fig. 2, which was related to the abductor digiti minimi muscle (Table 5).

Results from a PCA of the PCSA fractions are plotted in Fig. 3. PC1, PC2, PC3, and PC4 accounted for 55.1, 17.3, 9.6, and 6.3%, respectively. When a Kruskal–Wallis analysis for PC scores was performed, there were significant differences in the first three PCs for the PCSA fractions. The PCA of mass and PCSA fractions showed a similar tendency. Figure 3 demonstrates that orangutans were separated from humans and other great apes along PC1, which was related to the abductor hallucis brevis muscle and the first dorsal interosseous muscles (Table 5). Gorillas were separated from humans and other great apes along PC2, and humans from the great apes along PC3 (Fig. 3). *Post hoc* multiple comparisons indicated the PC1, PC2, and PC3 scores were significantly different between humans and orangutans, between chimpanzees and gorillas, and between humans and chimpanzees, respectively. The factor loadings were related to the abductor digiti minimi muscle for PC2 and the quadratus plantae muscle for PC3 (Table 5).

Discussion

Using multivariate analyses, we were able to distinguish and characterize some aspects of the intrinsic foot muscles of hominoids. In particular, a distinct pattern was seen in the orangutans, which occupied the positive position of PC1 in the PCA of the PCSA fractions (Fig. 3). This showed that the orangutans had the larger fraction of the first dorsal interosseous muscle and smaller fraction of the abductor hallucis brevis muscle (Tables 4 and 5). Particularly, in the orangutans, the first dorsal interosseous muscle had the greatest force-generating potential among all intrinsic foot muscles (Oishi et al. 2012; see also Table 4). These remarkable differences are not too surprising, as orangutans are phylogenetically and functionally differentiated from African apes and humans. Among great apes, the orangutans probably diverged more than 13 million years ago and have a very long period of separation from other hominoids (Page & Goodman, 2001; Raaum et al. 2005; Steiper & Young, 2006). The orangutans are fundamentally quadrumanous climbers in the rain forest canopy (Cant, 1987; Thorpe & Crompton, 2005, 2006) and their feet are extremely specialized for their function as a suspensory

Table 3 Comparisons of foot mass fractions among great apes and humans.

Abbreviation	Mass fraction (%)				
	Human (SD)	Bonobo	Chimpanzee (SD)	Gorilla (SD)	Orangutan (SD)
Hallucal muscles					
EHB	3.6 (0.56)	4.7	3.1 (0.49)	3.4 (0.67)	1.5 (0.86)
AHB	16.9 (0.13)	16.4	18.6 (3.31)	16.3 (1.38)	6.9 (1.36)
FHB	7.9 (0.93)	6.6	9.6 (0.85)	8.9 (0.43)	6.7 (1.39)
AH	12.0 (1.04)	20.0	19.1 (1.83)	15.7 (1.69)	15.3 (1.66)
Subtotal	40.4 (1.54)	47.7	50.4 (2.35)	44.4 (4.17)	30.4 (2.30)
Digiti minimi muscles					
ADM	10.2 (0.63)	7.6	5.5 (0.57)	12.1 (2.03)	4.8 (0.92)
FDMB & ODM	3.5 (0.41)	2.8	1.8 (0.11)	3.6 (0.17)	3.6 (0.82)
Subtotal	13.7 (0.23)	10.4	7.3 (0.64)	15.7 (1.86)	8.5 (0.73)
Intrinsic digital extensors					
EDB2	2.2 (0.14)	3.0	2.6 (0.41)	2.7 (1.00)	4.8 (1.07)
EDB3	1.3 (0.27)	2.0	2.3 (0.52)	2.3 (0.19)	3.1 (0.54)
EDB4&5	1.1 (0.03)	1.5	1.3 (0.84)	2.1 (0.55)	3.8 (0.87)
Subtotal	4.6 (0.44)	6.5	6.3 (0.80)	7.1 (1.74)	11.7 (1.53)
Intrinsic digital flexors					
FDB2	5.2 (0.24)	4.1	3.5 (1.48)	3.5 (0.77)	6.4 (1.55)
FDB3	3.9 (0.50)	6.1	5.1 (1.23)	5.8 (0.84)	5.5 (0.90)
FDB4&5	3.4 (0.33)	1.7	1.7 (1.33)	2.2 (0.62)	0.9 (0.90)
QP	8.7 (0.25)	0.5	NP	0.4 (0.50)	0.4 (0.76)
Subtotal	21.2 (0.17)	12.4	10.3 (2.30)	11.9 (1.19)	13.2 (2.16)
Interossei					
DI1	2.6 (0.61)	3.8	4.7 (1.68)	3.4 (0.29)	10.3 (1.17)
DI2	2.4 (0.45)	2.4	3.7 (0.76)	2.6 (1.07)	5.1 (1.01)
DI3	2.4 (0.45)	2.9	3.2 (0.51)	3.1 (0.24)	4.0 (0.57)
DI4	3.9 (1.03)	3.6	4.1 (1.11)	3.7 (0.16)	3.9 (0.52)
PI1	1.4 (0.42)	2.9	2.2 (0.25)	2.5 (0.19)	3.6 (0.75)
PI2	2.1 (0.02)	1.7	2.4 (0.31)	1.5 (0.26)	2.5 (0.36)
PI3	2.1 (0.09)	1.6	1.7 (0.39)	1.5 (0.26)	1.4 (0.40)
Subtotal	16.9 (2.86)	18.7	22.0 (3.61)	18.2 (2.08)	30.7 (3.00)
Lumbricals					
Lu1	0.9 (0.28)	1.2	1.0 (0.30)	0.5 (0.19)	1.3 (0.70)
Lu2	0.8 (0.36)	1.2	1.0 (0.21)	1.0 (0.29)	2.0 (0.33)
Lu3	0.9 (0.28)	1.0	1.1 (0.33)	0.7 (0.17)	1.5 (0.30)
Lu4	0.8 (0.44)	1.0	0.6 (0.27)	0.6 (0.13)	0.8 (0.24)
Subtotal	3.3 (1.36)	4.3	3.7 (0.53)	2.8 (0.78)	5.6 (1.18)

In two chimpanzees (C3 and C4), the abductor digiti minimi muscle (ADM), the flexor digiti minimi brevis muscle (FDMB), and the opponens digiti minimi muscle (ODM) were fused with one another (Oishi et al. 2012). Therefore, we measured the total mass of the three muscles for those two individuals and divided the mass into two groups (ADM and FDMB + ODM) based on the mass ratio obtained from other three chimpanzees (75.4 and 24.6%, respectively). Total and subtotals don't necessarily add up, due to rounding error. NP, muscle not present. Standard deviations (SD) are shown in parentheses. Muscle name abbreviations are as detailed in Table 2.

supporting organ among extant hominoids, as reflected in the rudimentary hallux, the elongated and curved lateral four toes, and the quite inverted foot posture (Schultz, 1963; Tuttle, 1970; Lewis, 1980a,b; Gomberg, 1981, 1985; Rose, 1988; Marchi, 2010; Kanamoto et al. 2011). In response to these specializations of the orangutan foot, a comparatively larger force may act on the digit II for secure prehension of branches in hook-like gripping. Therefore, this force might be countered by the first dorsal interosseous muscle, whose tendon runs on the medioventral

aspect of the second metatarsophalangeal joint and acts as a flexor of the second toe (Boyer, 1935; Tuttle, 1970; see also Fig. 1). Morphological discriminations in the intrinsic muscles of the orangutans seem to reflect the different strategy of foot use during arboreal locomotion.

The gorillas tended to be distinguished from other hominoids along PC2 (Fig. 3), indicating that this species was characterized by the larger PCSA fraction of the abductor digiti minimi muscle (Tables 4 and 5). Although the locomotor patterns show similar tendencies among African apes

Table 4 Comparisons of foot PCSA fractions among great apes and humans.

Abbreviation	PCSA fraction (%)				
	Human (SD)	Bonobo	Chimpanzee (SD)	Gorilla (SD)	Orangutan (SD)
Hallucal muscles					
EHB	3.0 (0.13)	3.2	2.2 (0.25)	2.4 (0.53)	1.0 (0.54)
AHB	14.3 (0.40)	9.0	12.6 (3.26)	8.7 (2.49)	4.5 (0.96)
FHB	8.5 (0.18)	8.1	11.2 (0.99)	10.7 (0.90)	8.7 (2.17)
AH	13.1 (1.34)	12.5	14.2 (1.97)	11.0 (4.67)	10.0 (1.82)
Subtotal	39.0 (0.89)	32.8	40.2 (3.64)	32.7 (8.59)	24.2 (3.41)
Digiti minimi muscles					
ADM	8.8 (0.76)	9.4	6.1 (0.82)	15.3 (1.74)	6.9 (1.91)
FDMB & ODM	4.0 (0.52)	5.7	4.6 (0.71)	5.4 (0.35)	6.2 (1.70)
Subtotal	12.8 (0.24)	15.2	10.7 (1.43)	20.7 (1.40)	13.1 (2.49)
Intrinsic digital extensors					
EDB2	1.9 (0.25)	2.0	1.8 (0.25)	1.3 (0.02)	3.2 (1.00)
EDB3	1.1 (0.05)	1.5	1.7 (0.60)	1.4 (0.05)	1.8 (0.19)
EDB4&5	1.0 (0.06)	1.4	1.1 (0.60)	1.3 (0.37)	2.3 (0.73)
Subtotal	4.0 (0.25)	4.8	4.5 (0.43)	4.0 (0.40)	7.3 (1.37)
Intrinsic digital flexors					
FDB2	4.3 (0.56)	2.3	2.0 (0.96)	1.8 (0.48)	3.8 (0.62)
FDB3	3.5 (0.27)	3.4	2.7 (0.47)	2.8 (1.01)	3.3 (0.62)
FDB4&5	3.3 (0.28)	2.5	1.8 (0.61)	2.4 (0.34)	1.4 (1.17)
QP	6.6 (0.20)	0.3	NP	0.2 (0.31)	0.2 (0.39)
Subtotal	17.7 (0.75)	8.5	6.4 (1.57)	7.1 (0.50)	8.7 (2.02)
Interossei					
DI1	3.7 (0.05)	5.9	7.0 (2.03)	4.4 (0.22)	12.9 (1.33)
DI2	3.1 (0.76)	5.1	6.2 (1.11)	5.5 (2.06)	7.3 (1.03)
DI3	3.4 (0.33)	4.9	5.2 (0.43)	5.6 (1.41)	6.7 (2.01)
DI4	5.6 (0.53)	6.5	6.0 (1.36)	7.1 (0.24)	6.2 (0.93)
PI1	2.6 (0.06)	6.1	3.7 (0.43)	5.3 (0.37)	6.2 (1.43)
PI2	2.8 (0.34)	4.1	4.5 (1.34)	2.9 (1.87)	3.3 (0.57)
PI3	2.8 (0.30)	3.7	3.5 (0.95)	3.1 (1.17)	2.0 (0.63)
Subtotal	24.1 (2.37)	36.3	36.1 (4.82)	33.8 (6.60)	44.6 (4.98)
Lumbricals					
Lu1	0.6 (0.07)	0.6	0.5 (0.15)	0.4 (0.22)	0.5 (0.20)
Lu2	0.8 (0.30)	0.7	0.6 (0.20)	0.6 (0.17)	0.7 (0.15)
Lu3	0.6 (0.10)	0.5	0.6 (0.20)	0.4 (0.08)	0.5 (0.12)
Lu4	0.5 (0.09)	0.6	0.3 (0.12)	0.3 (0.03)	0.3 (0.12)
Subtotal	2.4 (0.23)	2.4	2.0 (0.41)	1.6 (0.49)	2.1 (0.43)

In two chimpanzees (C3, and C4), the abductor digiti minimi muscle (ADM), the flexor digiti minimi brevis muscle (FDMB), and the opponens digiti minimi muscle (ODM) were fused with one another (Oishi et al. 2012). Therefore, we measured the total PCSA of the three muscles for those two individuals and divided the PCSA into two groups (ADM and FDMB + ODM) based on the PCSA ratio obtained from other three chimpanzees (57.4 and 42.6%, respectively). Total and subtotals don't necessarily add up, due to rounding error. NP, muscle not present. Standard deviations (SD) are shown in parentheses. Muscle name abbreviations are as detailed in Table 2.

(Doran, 1992, 1993; Doran & Hunt, 1994; Remis, 1995), the gorillas are the most terrestrial animal among extant hominoids, except for humans (Remis, 1995). The proximal articular surface of the metatarsal V bone of the gorillas has a dorsoplantar convex curvature, and tends to be mediolaterally narrower and a little more concave in curvature than that of the chimpanzees, suggesting that the lateral column of the gorilla foot dorsiflexes during terrestrial locomotion (Proctor, 2013). The abductor digiti minimi muscle has a relatively well-developed additional muscle belly (*M. abductor ossis metatarsi V*) in the gorillas (Straus, 1930; Raven, 1950); this portion is often found, albeit smaller, in the chimpanzees but is rare in the orangutans (Hepburn, 1892; Straus, 1930; Gomberg, 1981). The abductor digiti minimi muscle and its additional belly are located on the lateral side of the foot and insert onto the ventral aspect of the proximal phalanx of digit V and the lateroventral aspect of the base of metatarsal V, respectively (Straus, 1930; Raven, 1950; see also Fig. 1). Based on these anatomical placements, this muscular complex works against the external
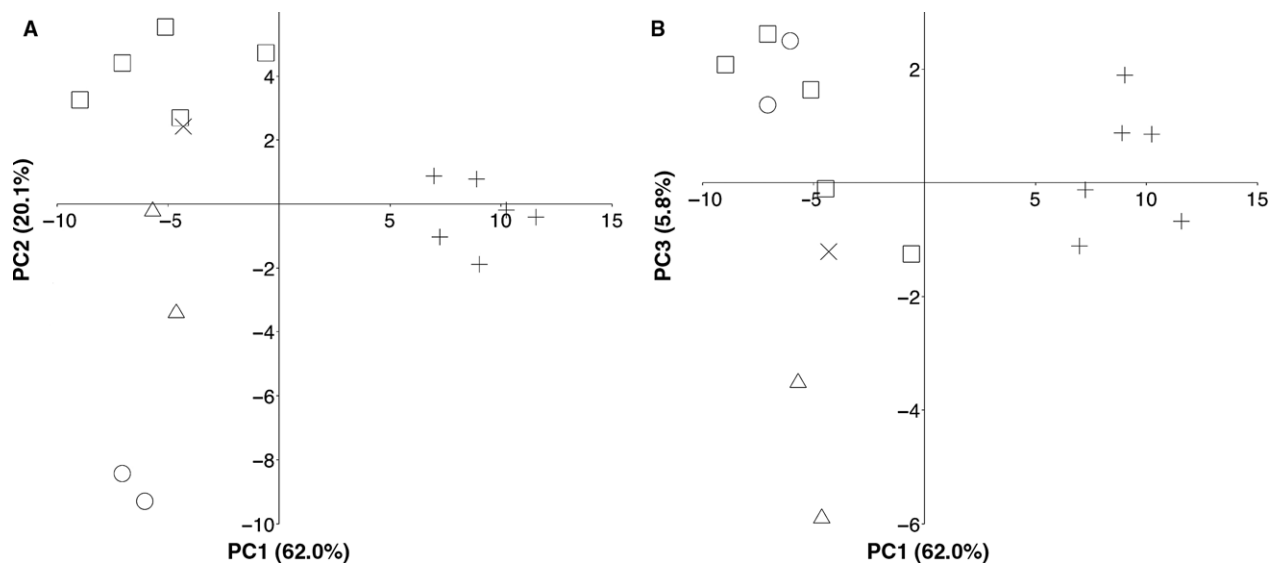
Fig. 2 Scatter plot of the principal component scores for mass fractions. (A) PC1 (x-axis) vs. PC2 (y-axis); (B) PC1 (x-axis) vs. PC3 (y-axis). The percentage of variance explained by each PC score is shown in parentheses. The markers are: (O) human, (□) chimpanzee, (×) bonobo, (△) gorilla, and (+) orangutan.

Table 5 Factor loadings for the intrinsic foot muscles.

Abbreviation	%Mass			%PCSA			
	PC1	PC2	PC3	PC1	PC2	PC3	PC4
Hallucal muscles							
EHB	−0.13	−0.01	−0.04	−0.11	−0.03	0.02	0.08
AHB	−0.75	0.19	0.28	−0.64	0.25	0.01	−0.31
FHB	−0.14	0.12	−0.10	−0.11	0.05	−0.50	0.05
AH	−0.09	0.61	−0.10	−0.26	0.27	−0.24	0.61
Digiti minimi muscles							
ADM	−0.20	−0.39	−0.73	−0.06	−0.85	−0.12	0.10
FDMB & ODM	0.06	−0.13	−0.09	0.10	−0.02	−0.13	0.25
Intrinsic digital extensors							
EDB2	0.15	0.02	0.11	0.09	0.10	0.12	0.04
EDB3	0.07	0.06	0.01	0.02	0.04	−0.04	0.02
EDB4&5	0.15	0.004	−0.11	0.08	0.02	−0.002	0.08
Intrinsic digital flexors							
FDB2	0.14	−0.13	0.26	0.04	0.05	0.33	0.07
FDB3	0.03	0.06	−0.24	0.02	−0.002	0.11	−0.01
FDB4&5	−0.10	−0.12	0.04	−0.08	−0.04	0.17	−0.02
QP	−0.12	−0.59	0.42	−0.16	−0.07	0.65	0.12
Interossei							
DI1	0.45	0.11	0.13	0.56	0.31	0.04	0.10
DI2	0.14	0.07	0.05	0.20	0.04	−0.20	−0.28
DI3	0.08	0.03	−0.01	0.18	−0.02	0.02	−0.34
DI4	0.01	0.01	−0.01	0.04	−0.09	−0.09	0.04
PI1	0.10	0.04	−0.05	0.19	−0.11	−0.01	−0.03
PI2	0.03	0.02	0.10	−0.01	0.07	−0.10	−0.41
PI3	−0.03	−0.02	0.05	−0.08	−0.01	−0.09	−0.21
Lumbricals							
Lu1	0.03	0.01	0.03	−0.004	0.01	0.003	−0.01
Lu2	0.06	0.02	−0.004	0.001	0.01	0.02	0.04
Lu3	0.03	0.02	0.03	−0.001	0.02	0.01	0.01
Lu4	0.01	−0.01	−0.01	−0.002	−0.002	0.02	0.02

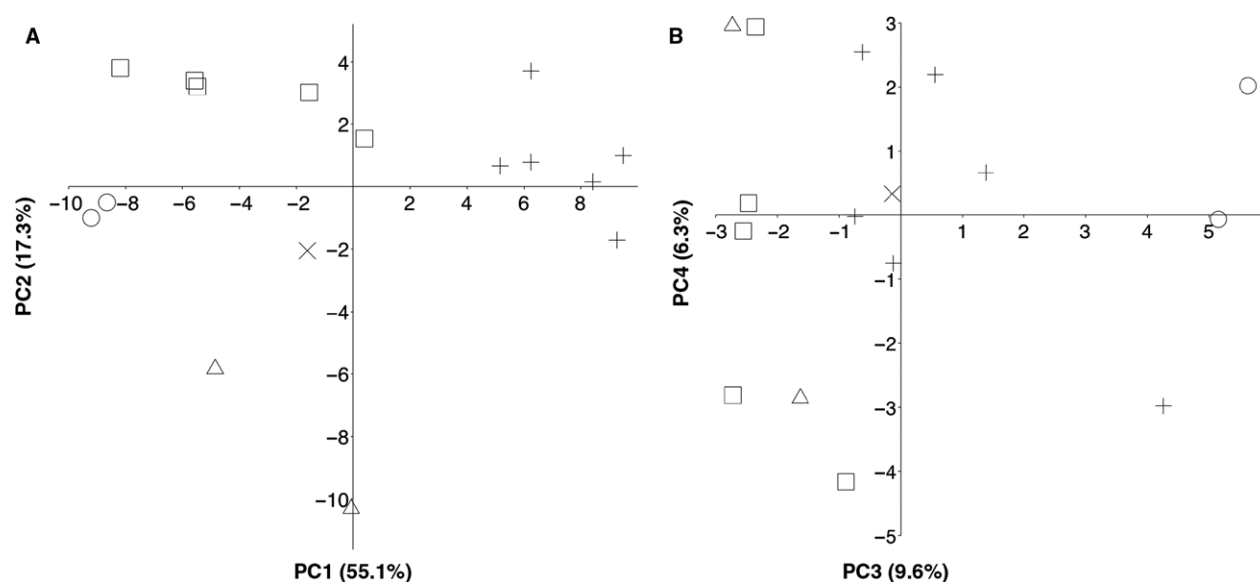Muscle name abbreviations are as detailed in Table 2.

Fig. 3 Scatter plot of the principal component scores for PCSA fractions. (A) PC1 (*x*-axis) vs. PC2 (*y*-axis); (B) PC3 (*x*-axis) vs. PC4 (*y*-axis). The percentage of variance explained by each PC score is shown in parentheses. The markers are: (O) human, (□) chimpanzee, (×) bonobo, (△) gorilla, and (+) orangutan.

dorsiflexion moment around the fifth tarsometatarsal joint. Therefore, although we are unable to test its function during walking on the ground, these features concerning digit V imply that the larger PCSA fractions of the abductor digiti minimi muscle may also contribute to dynamically supporting the lateral column of the gorilla foot. However, it has recently been suggested that gorillas may be more arboreal than previously thought (Crompton, 2016). Kinematics and biomechanics of the gorilla foot during terrestrial and arboreal locomotion should be investigated to identify the functional significance of the characteristic foot musculature in gorillas in future studies.

Among extant hominoids, humans are the only species that adopts habitual bipedal walking and does not retain the power gripping capacity of the foot (Aiello & Dean, 1990; Harcourt-Smith & Aiello, 2004). On the other hand, great apes frequently climb trees and share opposable halluces and long lateral toes as adaptations for secure prehension of arboreal substrates (Schultz, 1963; Tuttle, 1970; Lewis, 1980a,b Aiello & Dean, 1990). Based on the above considerations, it was expected that there would be large differences in the muscle architecture between humans and African apes. However, contrary to our expectation, humans and African apes had similar PC1 scores. Humans were found to be distinguished from other hominoids along PC3 in the PCA of the PCSA fractions, but not along PC1 (Fig. 3). This finding implies that functional differences in intrinsic foot muscles between bipedal humans and quadrupedal African apes are smaller than those between African apes and quadrumanous orangutans. The fact that bipedal human and quadrupedal African apes showed comparatively similar PC1 scores, possibly demonstrated that

phylogenetic history largely constrained the muscle architecture of the intrinsic foot muscles. Nevertheless, the factor loadings of PC3 in the PCA of the PCSA fractions demonstrated that humans were separated from great apes as a result of a relatively larger force-generating capacity of the quadratus plantae muscle (Fig. 3, Tables 4 and 5). These observed tendencies are in agreement with previously published qualitative anatomical research. Humans have the large two-headed quadratus plantae muscle, which originates from the calcaneus to the tendon of the flexor digitorum longus muscle (Gomberg, 1981; Aiello & Dean, 1990), whereas in great apes, this muscle, if present, is frequently absent or vestigial and single-headed (Straus, 1930; Boyer, 1935; Tuttle, 1970; Gomberg, 1981). The intrinsic plantar muscles play a critical role in dynamically supporting the plantar arch and midfoot rigidity, as well as maintaining body balance in human bipedalism (Reeser et al. 1983; Fiolkowski et al. 2003; Goldmann & Brüggemann, 2012; Kelly et al. 2012, 2014). Although this activity was reported to be modest, the activity tends to increase during dynamic locomotion (e.g. jogging or running; Reeser et al. 1983). Therefore, the relatively larger PCSA of the quadratus plantae muscle seems to be adapted to bipedal locomotion in humans.

Both African apes and humans occupied a negative position along PC1 in the PCA of the PCSA fractions (Fig. 3), resulting from larger PCSA fractions of the abductor hallucis brevis muscle than in the orangutans (Tables 4 and 5). African apes possess a longer and more mobile hallux than humans (Schultz, 1963; Tuttle, 1970; Lewis, 1980a,b Aiello & Dean, 1990), and its abduction contributes to the maintenance of balance during arboreal and terrestrial locomotion

(Vereecke et al. 2003). On the other hand, despite the loss of abduction of the hallux, the abductor hallucis brevis muscle in humans provides support for the medial longitudinal arch during bipedal walking (Reeser et al. 1983; Fiolkowski et al. 2003; Kelly et al. 2012, 2014). Therefore, although its functional meaning likely is different, a higher force-generating capacity of the abductor hallucis brevis muscle in both African apes and humans is not in conflict with the functional demands during each species' habitual locomotion. However, along PC1 in the PCA of the PCSA fractions (Fig. 3), African apes clustered closer to the orangutans, whereas humans took the most negative position, as a result of the relatively larger PCSA fractions of the interosseous muscles (especially the medial components) in African apes, but not as much in the orangutans (Table 4). These muscles act as abductors or adductors and also as flexors of the lateral toes and thus are responsible for power gripping by the foot (Straus, 1930; Sokoloff, 1972; Gomberg, 1981; Vereecke et al. 2005; see also Fig. 1), suggesting that the higher force-generating capacities of African apes should be interpreted as being related to the retention of arboreal adaptations. Taken together, these features suggest that the intermediate position of African apes along PC1 in the PCA of the PCSA fractions reflects a compromise between arboreal and terrestrial locomotions.

Although the present study included only one bonobo, our PCA results demonstrated that the PCSA fractions of the intrinsic foot muscles of the bonobo appeared to have a similar pattern to those of the chimpanzees, as described for the extrinsic foot muscles (Payne et al. 2006; Myatt et al. 2011). Although opportunities to obtain ape cadaveric material are very limited, it will be important to take these chances when they arise in order to confirm these results in a larger number of cases.

As noted above, the present study demonstrated that the orangutans are the most distinctive in muscle architecture among the great apes, and human muscle architecture is more similar to that of the African great apes (Figs 2 and 3). These results possibly suggest that muscle architecture differences between the species may also be driven by phylogenetic distance. Among the great apes, the orangutans diverged first more than 13 million years ago, then the gorillas diverged about 9 million years ago, and the chimpanzees about 7 million years ago (Hara et al. 2012). This phylogenetic relationship seems to correspond somewhat to the differences in muscle architecture among the great apes demonstrated in the figures, indicating that phylogeny could also be a strong determinant of foot muscle architecture along with the differences in locomotor behaviors.

In conclusion, this report contains, to our knowledge, the first multivariate analysis of relative foot muscle parameters among hominoids. This statistical method was advantageous for segregating many of the hominoid groups from the others, and it revealed several morphological differences in the intrinsic foot muscles between humans and the great apes. Some of these differences have previously been demonstrated by other qualitative and quantitative research, but this study adds important new contributions to our understanding of hominoid foot muscles. This procedure is useful for comparative studies designed to determine morphological adaptations specific to taxonomical groups and might also be applied to research involving structure–function relationships of other locomotor systems, e.g. the hands (Ogihara et al. 2005; Ogihara & Oishi, 2012).

Acknowledgements

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